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Gas transport through the root–shoot transition zone of rice tillers

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Abstract

Rice plants (*Oryza sativa* L.) are mainly cultivated in flooded paddy fields and are thus dependent on oxygen transport through the plant to maintain aerobic root metabolism. This gas transport is effectuated through the aerenchyma of roots and shoots. However, the efficiency of gas transport through the root–shoot transition zone is disputed and there are indications that the root–shoot transition zone may represent one of the largest resistances for gas transport. Therefore, we present gas conductance measurements of the root–shoot transition of individual rice tillers measured using SF_6. SF_6 was detected with a highly advanced laser based photoacoustic detection scheme allowing sensitive, high resolution measurements. In conjunction with these measurements, various plant morphological parameters were quantified. These measurements indeed indicate that the conductance at the root–shoot transition may be much smaller than the conductance of root and shoot aerenchyma within the rice plant. Conductance was strongly correlated to tiller transverse area. After elimination of tiller area from the conductance equation, the resulting permeance coefficient was still correlated to tiller area, but negatively and related to the process of radial tiller expansion. In addition, a decrease in the permeance coefficient was also observed for increasing distance from the plant centre. No correlation was found with tiller type or age of the mother tiller. Incorporation of estimates of the conductance of the root–shoot transition zone coupled to plant morphological parameters will allow considerable improvement of understanding and models on gas transport through plants.

Introduction

Rice (*Oryza sativa* L.) is one of the most abundant food crops in the world. The harvested area of rice in Asia comprised 132 million hectares in 1990 (Denier van der Gon, 2000). Rice is predominantly grown in flooded paddy fields of either irrigated or rain fed areas, which eliminates oxygen diffusion through the soil to the roots. Due to oxygen consumption by roots, aerobic microorganisms and soil fauna the oxygen concentration in the soil is depleted and the plants form additional aerenchyma in roots and shoots to provide a path way for oxygen to the roots necessary for aerobic respiration (Jackson and Armstrong, 1999). This capability of the rice plant to transport gas is essential to survive

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submerged conditions (Armstrong, 1979; Colmer 2003; Jackson and Armstrong, 1999).

Gas transport in rice plants is a diffusive process (Barber et al., 1962; Beckett et al., 1988) and is usually measured for entire plants (e.g., Aulakh et al., 2000b; Butterbach-Bahl et al., 1997; Hosono and Nouchi, 1997; Lee et al., 1981; Schütz et al. 1989). These investigations have provided important insights in the importance of internal plant gas transport for plant functioning and soil-atmosphere gas exchange (as reviewed, e.g., by Armstrong, 1979; Colmer, 2003; Nouchi and Mariko, 1993) and showed how gas transport rates are related to, e.g., temperature (Hosono and Nouchi, 1997), redox conditions (Kludze et al., 1993) and rice cultivar (Aulakh et al., 2000a). Such whole plant measurements do, however, not explain or quantify the bottlenecks of gas transport within plants. Gas transport through the rice plant is effectuated through a serial circuit of flows from the atmosphere through shoot aerenchyma, through a root–shoot transition, through root aerenchyma and to some degree across a root barrier. The latter is formed at flooded conditions (Colmer et al., 1998) and may result from sclerenchymatous fibres with thick secondary walls (Clark and Harris, 1981) and represents a physical barrier to gas losses from the root (Colmer, 2003). To understand the role of each part within the circuit, the diffusion conductance (or its reciprocal, the diffusion resistance) of individual tillers and especially parts thereof should be quantified. Hitherto, this has not been done, although correlations between whole plant gas transport capacities and aerenchyma (Aulakh et al., 2000b) and tiller number (Aulakh et al., 2000a) have been presented.

According to Butterbach-Bahl et al. (1997) the root–shoot transition zone represents the most important resistance to gas transport in rice plants. The qualitative data of Butterbach-Bahl et al. (1997) are, however, hard to use for quantitative purposes given their use of the Poisseuille equation (which is suitable for convective flows, but not for diffusive flows). On the other hand, a similar conclusion on the importance of the root–shoot transition zone was drawn from data by Hosono and Nouchi (1997). In contrast, Aulakh et al. (2000b) disregarded the root–shoot transition zone as an important resistance to gas transport based on good correlations between total gas transport rates and aerenchyma extent in the internodal region of the rice culm, although they did not find continuous aerenchyma between root and culm. Given the potential importance of the root–shoot transition zone for total gas transport through plants, quantitative data on this subject are needed.

In this paper, we present for the first time quantitative conductance measurements on the root–shoot transition of individual tillers. The aims of this research were (1) to quantify the conductance of this potentially important part of gas transport through rice plants and (2) to understand the causes in its variability amongst tillers from plant morphological measurements. Sensitive measurement on the gas conductance were made possible by the application of a novel sensitive detection method, a highly advanced laser based photoacoustic detection scheme, to determine concentrations of an inert tracer gas, SF_6.

Materials and methods

Plant material

Rice plants (*Oryza sativa* L.) of the IR72 cultivar were grown in the greenhouse under natural local daylight conditions (15 MJ m^{-2} d^{-1} for 1998). Plants between 106 and 143 days old at the end of the heading stage were used in our experiments. The temperature in the greenhouse was 19 ± 2 °C.

The plants were grown in soil with an equal mixture of rice paddy soil (Philippines) and river clay (The Netherlands). Seedlings were planted in large plastic trays with 23 cm of spacing between the plants (six plants per tray, 0.2 m^3). A layer of three-centimetre of water was maintained on top of the soil throughout cultivation.

The tiller emergence date, i.e. the date at which a tiller separated from its mother tiller, was registered and the tiller itself labelled (numbered successively). The tiller age used in the experiments is the time span between labelling of the tiller and the actual conductance measurement. Together with the emergence date, the tiller number of the mother tiller was recorded. This was used to classify the tillers in tiller types, being the main stem, primary, secondary, tertiary etc. tillers. The main stem originates from the

seed, a primary tiller emerges from the main stem, the secondary tiller from the primary, the tertiary from the secondary etc. (Counce et al., 1996). From these data the age of the mother tiller, at the moment at which the new tiller is produced, was calculated. Finally the tiller position, obtained by classifying the tillers according to 6 different concentric rings around the centre of the plant, was determined. We numbered the rings from 1 to 6 from the centre outwards.

Experimental set-up

The plants used in the experiment were removed from their pots and the soil around the roots was gently washed away. The root–shoot transition zone of the plant was wrapped in tissue paper and fitted in a glass tube (with two open-ends). Liquefied gelatine (at about 40 °C; Oxoid L8, Merck 4070, Haarlem, The Netherlands) was poured in small portions saturating the paper plug. Each portion was allowed to solidify before the next was applied making an airtight seal by filling the air spaces between the tillers (Figure 1). The lower part of the glass cylinder was put in a glass vessel containing a small quantity of water to make an airtight seal with a 'water lock' (Figure 1). After this preparation, the roots and the shoots were cut; leaving approximately 5 cm of roots and 10 cm of shoots attached to the transition zone. Such lengths were needed to prevent damage (for thin tillers) during preparation and measurement. For each measurement, one tiller was selected and placed inside a sampling cuvette over the top end of a tiller (Figure 1). At the bottom, the sampling cuvette was sealed airtight around the tiller by the gelatine. The other tillers could freely exchange gases with the lab air (with tracer gas concentration ≈ 0).

A carrier flow of 1–3 l h^{-1} of air was flushed through the sampling cuvette. Caution was taken to avoid pressure differences between the cuvette and the lab air as result of the air flow (air was pumped through the detection system and the pressure in the flow was equalised to atmospheric pressure just before the sampling cuvette by the combination of an exhaust and a pump at the end of the line. The flow through the exhaust was a few ml h^{-1} so that the flow resistance was negligible). Gas transport through the root–shoot

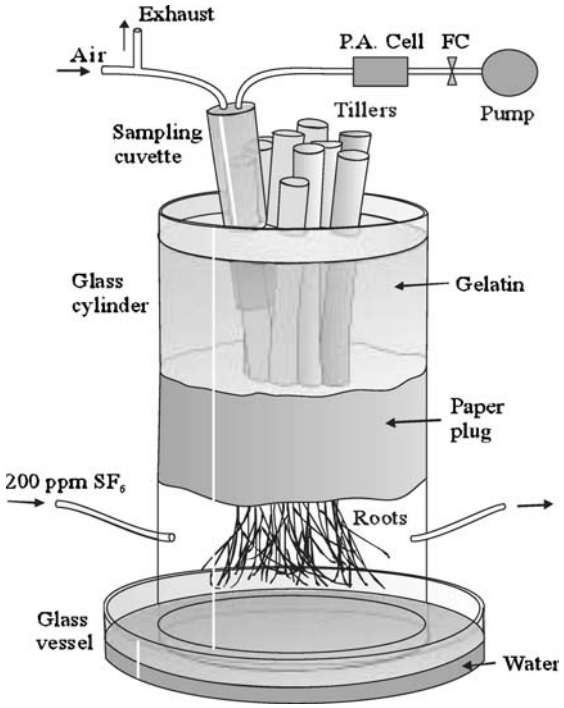

Figure 1. Set-up for the conductance measurement of individual tillers on an intact root–shoot transition zone (of one plant). Through the lower compartment flushes a flow of 200 ppm of SF_6 in air; a water lock closes this part. A sampling cuvette collects the gas emitted by one tiller. The other tillers emit freely to the lab-air.

transition zone was measured with SF_6 as a tracer gas. SF_6 is a non-toxic (Anonymous, 1976), biologically inert tracer gas (Johnson et al., 1994) that could be sensitively detected. A constant SF_6 concentration in the lower part of the glass cylinder was obtained by a constant gas flow of an SF_6-air mixture at a concentration of 200 ppm (parts per million by volume = 10^{-6} m^3 m^{-3}). Measurements were taken at steady state, which was obtained typically 20 min after positioning the sampling cuvette. After measurement, the tiller transverse area (A_{til}) was determined by calliper measurements assuming oval geometry. In addition, slices of plant tissue of the root–shoot transition zone were isolated and soaked overnight in a lactic acid (85%), chloral hydrate, phenol, clove oil and xylene solution (2:2:2:2:1 by weight, Herr, 1971). Interference phase contrast pictures were taken of the root–shoot transition at high resolution complementary to those existing at

lower resolutions (Aulakh et al., 2000b; Butterbach-Bahl et al., 2000) to determine the possible presence of small lacunae in the root–shoot transition zone.

In an additional experiment, the root–shoot transition zone of one plant has been subjected to a pressure difference of several milibars by restricting the outflow of the lower compartment. The difference in water level at the 'water lock' indicated the overpressure. The conductance of seven tillers has been measured this way and was used to quantify average pore diameter at the root–shoot transition zone by Poisseuille law (Groot, 2002).

In both experiments, SF_6 was detected with the laser-based photoacoustic trace gas detection method. This method is a sensitive on-line technique to detect extremely low gas concentrations in ambient air (Harren & Reuss, 1997). Here, we used a CO_2-laser that emits radiation at 90 laser lines in the infrared region of the electro-magnetic spectrum (wavelength 9–11 μm). This method sensitively detects gases that possess high absorption strength in this wavelength region combined with a characteristic absorption pattern. By comparing the photoacoustic signals on different laser lines (i.e. different absorption strengths of the gas under investigation), the response of the gas can be separated from other, interfering signals which do not show the same pattern (Bijnen et al., 1996). The integration time for a concentration determination is about 1 min.

At atmospheric pressure a large number of rotational SF_6 lines overlap with the CO_2-laser line at 947.74 cm^{-1} (10P16) resulting in high absorption strength of 0.85 $Torr^{-1}$ cm^{-1} (646 atm^{-1} cm^{-1}) (Cox & Gnauck, 1980). With our photoacoustic set-up we are able to detect SF_6 concentrations down to 5 parts per trillion by volume (1 ppt $= 1 \times 10^{-12}$ m^3 m^{-3}).

Calculations

The diffusive flow of SF_6 through the tiller (Φ_D, mol s^{-1}) mixes with the carrier flow (ϕ_{car}, m^3 s^{-1}) through the sampling cuvette towards the detection cell (ϕ_{PA}, m^3 s^{-1}). This is expressed by:

$$C_{car}\phi_{car} + \Phi_D = C_{PA}\phi_{PA}, \qquad (1)$$

where C_{car} is the SF_6 concentration (mol m^{-3}) in the carrier flow before it entered the sampling cuvette and C_{PA} the concentration in the carrier flow after the sampling cuvette measured by the photoacoustic system. Because the carrier flow does not contain any SF_6, $C_{car} = 0$ (mol m^{-3}) we get:

$$\Phi_D = C_{PA}\phi_{PA} \qquad (2)$$

In the experiments C_{PA} is measured and ϕ_{PA} is known.

The diffusive flow through the root–shoot transition zone of a rice plant tiller (Φ_D) occurs via small pores. Fick's law describes the combined gas diffusion through all these pores:

$$\Phi_D = D\Delta C \sum_{i=1}^{i=N} \left(\frac{A_p}{l_p}\right)_i, \qquad (3)$$

where D is the diffusion coefficient (m^2 s^{-1}), ΔC the concentration difference between roots and tillers (mol m^{-3}), N the number of pores in the root–shoot transition zone of the tiller, A_p the transverse area of a single pore (m^2) and l_p its length (m).

In the experiments ΔC was not completely constant as it was manipulated through our experimental set-up and thus unwanted in a comparison of the tiller conductance. Therefore, we define conductance κ as:

$$\kappa = \frac{\Phi_D}{\Delta C} = D \sum_{i=1}^{i=N} \left(\frac{A_p}{l_p}\right) \qquad (4)$$

Note that, when comparing diffusive flows with electrical current, ΔC is the analogue of ΔV the voltage and Φ_D the analogue of I the electrical current. From this we see that the conductance parameter $\kappa = \Phi_D/\Delta C$ is the reciprocal of the resistance. The right hand side of Eq. (4) represents the combination of the diffusion coefficient with unknown plant morphological variables. This expression thus allows testing the combined effects of plant morphology on gas conductance.

Unfortunately, A_p and l_p are unknown – and probably variable – morphological parameters, which makes it difficult to interpret the dynamics of κ. Therefore, to eliminate these unknowns from Eq. 4, κ is linked to the generally available plant morphological parameter A_{til}, the tiller

transverse area measured at cutting point, by defining the Permeance coefficient P (m s^{-1}) as:

$$P = \frac{\Phi_D}{A_{til}\Delta C} \quad (5)$$

Expressing the conductance per unit tiller area effectively eliminates the dependence of conductance on surface area. A_{til} was chosen as an approximation of A_p as it is proportional to the total surface area of lateral roots (Matsuo and Hoshikawa, 1993), which is presumably again proportional to $\sum A_p$. Given the lateral expansion of tillers and the predominantly lateral transport of gases in the root–shoot junction (Aulakh et al., 2000b), this measure provided a more constant estimates of P than, e.g., the number of roots (results not shown). In addition, the use of A_{til} in this calculation of P is fully compatible with the calculation of the permeance coefficient P through cuticles that also divides by the overall (leaf) area instead of the actual area through which compounds are exchanged (Becker et al., 1986; Kerstiens, 1996). Moreover, this definition allows prediction of P based on general plant morphology. Note that both κ and P depend on the diffusion coefficient of the used tracer gas (D_{SF6} = 1.04 10^{-5} m^2 s^{-1} at 20 °C (Borchers et al., 1969)). Using another tracer gas, therefore, requires κ and P to be corrected for the diffusion coefficient.

Statistics

Prior to further statistical analysis the distribution of κ and P was tested for normality and homogeneity of the residuals. No transformation was necessary. The effect of the plant under investigation on κ and P was tested by a one-way ANOVA and by an ANCOVA with additionally tiller area and tiller age as covariates. The effects of tiller age and tiller area on κ and P were tested by Pearson's correlation followed by backward regression. The effect of time after plant cutting on κ was tested by a paired t-test with the initial and the final measurements, respectively, as groups. The effect of tiller type on P was tested by a one-way ANOVA. Finally, the effect of position within the plant on P was tested by linear regression.

Results

Plant morphology

Tiller transverse area vs tiller age showed an expansion in tiller area for young tillers (Figure 2). This expansion in area stopped 60 days after the tiller separated from its mother tiller. Older tillers had a more or less constant area, independent of tiller age. The end of the radial tiller expansion was not related to the formation of new tillers, which occurred at any time from 20 to 120 days (data not shown).

An interference contrast picture (Figure 3) taken of the root–shoot transition zone clearly shows that there is no aerenchyma present at the root–shoot transition zone. Instead, root aerenchyma decreased to zero in the basal regions, where the root cortex converged with the shoot cortex. This indicates that gases have to pass through small inter-cellular spaces from root to shoot and vice versa. This was confirmed by the pressurized flow experiments from which pore radii of 2.5 ± 1.8 μm were calculated using Poisseuille law.

Gas conductance and permeance coefficient

Given that different tillers from different plants had been measured, it was tested whether κ was affected by the plant under investigation. This effect was insignificant ($P > 0.10$). This effect was also insignificant ($P > 0.10$) in an ANCOVA analysis with tiller area and tiller age as covariates. In another control analysis, the effects of potential changes in plant performance in time after cutting roots and shoots on measured gas conductance were analysed. For this analysis on artefacts the conductance of 15 tillers with a maximal spread in tiller age was measured twice over, on average, a 4 h period. The measured κ was not significantly different over time ($P = 0.80$). Conductance was thus not inevitably changed between 15 min (the average time needed to prepare the initial measurement) and, on average, 4¼ h after cutting.

Both tiller age ($P = 0.019$) and tiller area ($P < 0.001$) were significantly correlated to κ. The effects of these parameters could not be separated given its collinearity (see Figure 2), but

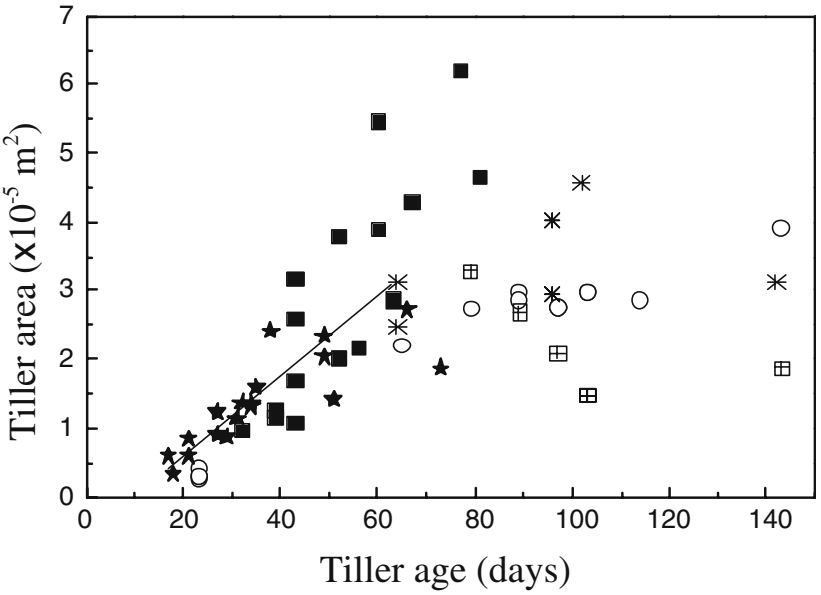

Figure 2. Plant morphology dynamics: Tiller transverse area A_{til} as function of tiller age at the day of measurement. Different symbols represent different plants, the lines represents a significant ($P < 0.05$) regression line over the total set for tillers younger than 60 days.

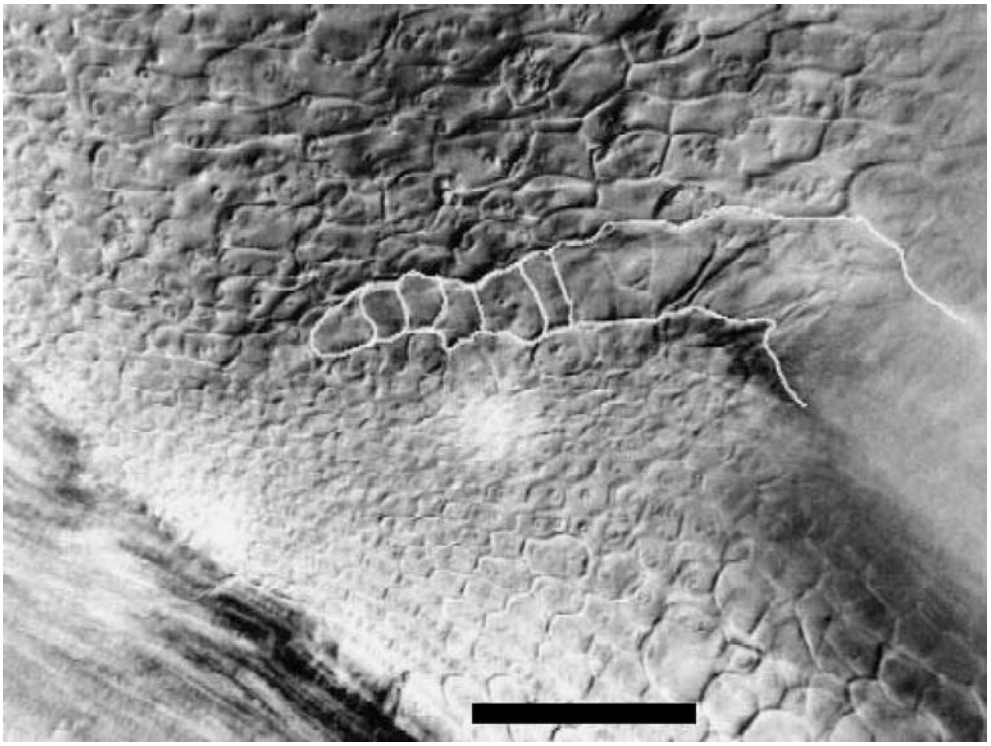

Figure 3. Interference contrast picture of the root–shoot transition zone taken in longitudinal direction. The root cortex (bottom right) converges with the central cylinder at the transition to the cortex of the tiller (top). A subepidermal layer of the root extends into the tiller cortex (emphasised by a white line). At the left bottom a part of the central cylinder of the root is visible. Root and shoot aerenchymas are both outside the picture. The bar is 100 μm.

tiller age was eliminated in a backward regression with both parameters, suggesting that tiller area was the dominant morphological parameter affecting κ (Figure 4).

Tiller area was eliminated in the permeance coefficient P and similar to κ, P was unaffected by the plant under investigation ($P > 0.50$). Tiller type (primary or secondary tiller) did neither significantly ($P > 0.50$) affect P. However, there was a significant ($P = 0.006$), but for this parameter negative, correlation between P and tiller area (Figure 5a). The pattern of P with tiller age was undirected and insignificant (Figure 5b). However for tillers younger than 60 days old (the age after which radial expansion stopped, Figure 2), P significantly ($P < 0.05$) decreased with tiller age, presumably again through the collinearity between tiller age and tiller area. In addition to tiller area, P was significantly ($P < 0.05$) related to the position of the tiller in the plant (Figure 5c). Apparently, P decreases for tillers in the outer regions of the plant (high ring number). No correlation between tiller age or tiller area and position was found (i.e. the age distribution of tillers in the plant is random), ruling out that this is a 'hidden' age relation.

Discussion

Importance of the root–shoot transition

The measured values for conductance κ for the root–shoot transition zone were orders of magnitude lower than conductance estimates of roots and shoots calculated in a gas transport model for rice plants (van Bodegom et al., 2001). Because 10-cm of shoot and 5-cm of root was still attached to the root–shoot transition zone in our experimental set-up, the effect on conductance of these additional tissues was quantified to test for potential artefacts. We thus calculated the conductances for the 10-cm shoot tiller and 5-cm root present in our set-up (without the root–shoot resistance) for comparison to our measured conductance. Given the diffusion barrier in the basal root in flooded systems (Colmer, 2003), the inertia of SF_6 and the negligible resistance to gas entry to the cut root, the length of the diffusion path way of gases will be the whole 5-cm root. Similarly, gases leave rice tillers through micropores absent in the bottom 10 cm (Nouchi and Mariko, 1993) and consequently, gases will travel the whole 10-cm shoot. In addition, we applied the diffusion coefficient of SF_6 of 1.04×10^{-5} m^2 s^{-1} at 20 °C (Borchers et al., 1969), a root aerenchyma fraction of 16–52% (Butterbach-Bahl et al., 1997; 2000; Kludze et al., 1994) and a shoot aerenchyma fraction of 38–45% (Butterbach-Bahl et al., 1997; Jensen et al., 1969). This results in a conductance in the cut shoot of $1.17 \pm 0.07 \times 10^{-9}$ m^3 s^{-1} and a conductance of the cut root of $1.92 \pm 1.02 \times 10^{-9}$ m^3 s^{-1}. This compares positively to the average κ of 0.05×10^{-9} m^3 s^{-1} (Figure 4). Firstly, this implies that the additional conductance hardly biased our measured conductances of the root–shoot transition zone: The root–shoot conductance (κ_{rs}) is the inverse of the diffusive resistance of the root–shoot transition zone (R_{rs} in s m^{-3}). The diffusive resistance of the root–shoot transition zone equals the measured resistance subtracted with the calculated resistances of the root and shoot parts:

$$R_{rs} = \frac{1}{\kappa_{rs}} = \frac{1}{\kappa_{meas}} - \frac{1}{\kappa_{shoot}} - \frac{1}{\kappa_{root}} \qquad (6)$$

This implies that the real κ_{rs} was on average 7% higher than the measured κ. Secondly, and more importantly, the calculations show that the root–shoot transition zone may be a by far stronger limiting factor to total plant gas transport than the tillers and the roots. The root–shoot junction had a much lower conductance than other plant compartments even though its length is much smaller than the length of tillers and roots. The

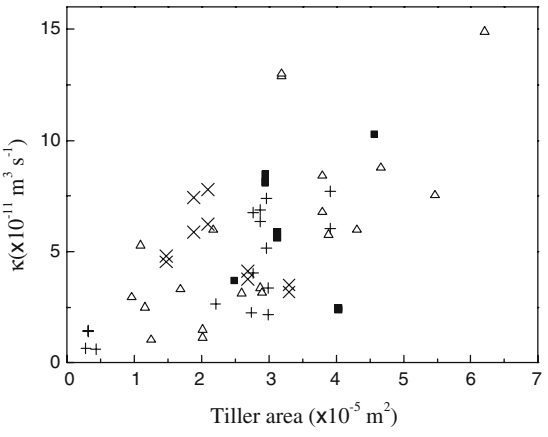

Figure 4. Conductance κ of SF_6 in the root–shoot transition zone as a function of tiller transverse area. Different symbols represent different plants.

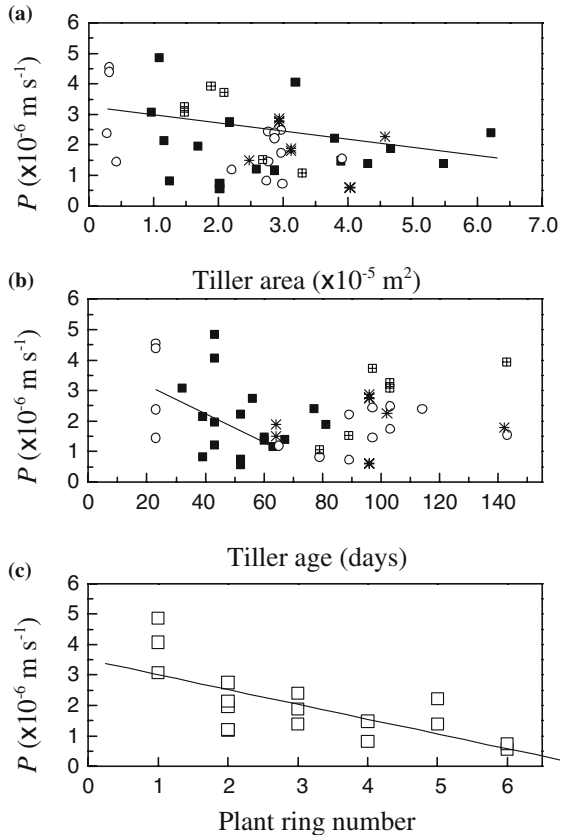

Figure 5. Dependence of the permeance coefficient P (in m s^{-1}) on plant morphological parameters for (a) The tiller transverse area A_{til}, (b) Tiller age and (c) as function of its position within the plant indicated by ring numbers 1–6. Tillers in the centre of the plant have the ring number 1 and tillers at the edge ring number 6. The lines represent significant ($P < 0.05$) regression lines.

length of the root–shoot junction was estimated to be about 0.24 ± 0.07 mm based on minimal distances between the aerenchymous tissues of roots and culm as measured from microscopic slices as in Figure 3, neglecting tortuosity. This length is implicitly accounted for in the calculations (see Eq. 4). This length difference should have led to higher conductance values for the root–shoot junction compared to the shoot and root compartments. For the conductance of the shoot and root compartments to become similar to the root–shoot junction, their lengths should increase further by a factor 24 and 38, respectively. Such lengths do not occur in modern rice varieties. On the other hand, the conductance across whole tillers and roots will be smaller than the ones for the cut parts calculated here given the larger lengths of complete tillers and roots and the non-uniform distribution of porosity across root length (e.g., Luxmoore et al., 1970). The transport length from culm to tiller micropores is about 20 cm (Nouchi and Mariko, 1993), which decreases tiller conductance to a value that still is 12 times higher than the root–shoot conductance. Average length of individual roots is about 40 cm (Matsuo and Hoshikawa, 1993), which leads to a root conductance of still 5 times higher than the root–shoot conductance. The potential consumption of gases (e.g., for O_2 by root respiration) might also decrease conductance by increased concentration differences. However, under influence of root respiration, root conductance is expected to decrease by 20% (Armstrong, 1971). Therefore, the root–shoot transition zone is considered an important transport obstruction, which merits its quantification, as presented for the first time in this paper.

The low conductance of the root–shoot transition zone is probably caused by the absence of continuous aerenchyma as shown in the microscopic pictures, forcing gases through intercellular spaces (Figure 3). This partly supports the findings by Aulakh et al. (2000b) who showed the presence of dense cell tissues at the transition zone. The pictures complement those by Butterbach-Bahl et al. (2000) who showed that the aerenchyma of roots and shoots was not connected, although the resolution of these pictures was too low to eliminate the possible presence of small lacunae. The absence of lacunae was confirmed through the pressurised flow experiment that yielded low flow rates through the root–shoot transition zone from which pore radii of 2.5 ± 1.8 μm were calculated. Such sizes correspond to intercellular spaces that have not been parted as a result of separation or collapse of intervening cells.

Effects of plant morphology on conductance at root–shoot transition

Given the limitations of the root–shoot transition zone to gas transport, it is important to determine its dependence on plant morphological parameters. Several patterns with plant morphological parameters can be distinguished. Firstly, conductance κ was positively correlated to tiller area, which is understood and expected from Eq. (3) although this does not explain whether the

effects of tiller area are due to l_p or A_p. To analyse the residual variation in conductance after correction for cross-sectional area, we defined P. In P, the cross-sectional area was approximated by tiller area, as A_p could not be quantified due to the small pore size (see results section) and the complicated spatial pore arrangement. In contrast to expectations, there was still a correlation to tiller area for P for young tillers, although the correlation was weaker and negative in that case (Figure 5a). In combination with the fact that correlation was absent for old tillers of which radial tiller expansion had stopped, this suggests that this decrease in P (for young tillers) might have been the result of the radial tiller expansion. Presumably, radial tiller expansion led to an increasing distance between root and shoot aerenchyma, thus increasing l_p, which directly decreases P (see Eq. (3) and (4)). The combination of a termination of radial tiller expansion with continuing aerenchyma development might also explain the slight increase in P with age for older tillers, although that trend was insignificant (Figure 5b). It was not driven by the development of new tillers, which were produced throughout the period (this paper; Counce et al., 1996) and neither by aerenchyma development (Jackson and Armstrong, 1999) as this should have led to an increase in P with tiller area.

Secondly, it was shown that neither κ nor P was related to the tiller type, i.e. whether the tiller was a primary, secondary or tertiary tiller.

Thirdly, it was shown that P was reduced for tillers in the outer regions of the plant (Figure 5c). A possible explanation for this observation is the higher density of tillers in the centre of the tussock as each tiller has its own roots emerging from the tiller and as each tiller is attached to neighbouring tillers at the root–shoot transition zone. Together, this might have led to more connections in the centre of the tussock, thus increasing conductance. Future research is necessary to elucidate the exact mechanisms uderlying the variability in the gas conductance through the root–shoot transition zone of rice.

Conclusions

This paper presented for the first time direct measurements on the gas conductance of individual tillers of the root–shoot transition zone in rice. These quantifications show that the root–shoot transition zone represents a major obstacle for gas transport. The conductance was related to and can be calculated from the tiller transverse area and to the position of individual tillers within the tussock. Given the importance of the root–shoot conductance in determining the overall plant gas transport conductance, the incorporation of these estimates into plant gas transport descriptions allows a better description and understanding of gas transport through plants. This allows considerable improvement of models on gas transport through plants, e.g., methane emission models, plant aeration models and rhizosphere models on O_2 and CO_2 dynamics for wetland plants.

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